

Altitudinal distribution and abundance patterns of bird species in the Eastern Arc Mountains, Tanzania

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The Eastern Arc Mountains of Tanzania are known as one of the worlds 'hot spots' for endemism and as an important focal area for the protection of birds (Burgess *et al.* 1998, Collar & Stuart 1988, Stattersfield *et al.* 1998). This species-rich archipelago of montane forests has been subject to a growing number of ornithological studies, and many aspects of species diversity (e.g. Stuart *et al.* 1993, Fjeldså & Rabøl 1995, Cordeiro 1998) and patterns of speciation and endemism (Fjeldså & Lovett 1997, Roy *et al.* 1997) have recently been analysed on a regional scale. The biodiversity riches of these unique forests have caused attention to be focused on identifying conservation priorities and preventing further degradation of the most important forest reserves (e.g., Hamilton & Bensted-Smith 1989, Newmark 1991, 1998, Rodgers 1993, Seddon *et al.* 1999).

Despite this interest many aspects of the forest bird communities remain unknown. Knowledge of the biogeography and altitudinal preferences of individual Eastern Arc species is generally limited to geographical and (to some extent) altitudinal distribution. A number of publications have also included notes on abundances at various altitudes (Sclater & Moreau 1932, Moreau 1940, Stuart *et al.* 1987, Jensen & Brøgger-Jensen 1992, Dinesen *et al.* 1993, Moyer 1993, Cordeiro 1994, Svendsen & Hansen 1995), summarised in the standard works of Britton (1980) and the 'Birds of Africa' series (Brown *et al.* 1982, Fry *et al.* 1988, Urban *et al.* 1986, 1997, Keith *et al.* 1992).

However, comparative studies that incorporate standardised measures of abundance are rare and cover only a few sites (Evans & Anderson 1993, Fjeldså *et al.* 1997, Fjeldså 1999, Seddon *et al.* 1999). This paper attempts to describe the abundance patterns of Eastern Arc bird species as a function of entire elevational gradients. The idea of 'mapping' the abundance of individual species according to altitude is not new. Terborgh (1971) used this approach to illustrate the relative importance of competition and ecotones in Andean birds. Able & Noon (1976) applied it to competing congeners in north-east America. To my knowledge, however, this is the first time that the altitudinal abundance patterns of an entire bird community have been documented in Africa.

Study area

The Eastern Arc Mountains stretch from the Taita Hills in south-east Kenya through Tanzania to the Makambako Gap south-west of the Udzungwa Mountains (Figure 1) (Lovett 1990, Stattersfield *et al.* 1998). Avifaunally, however, the Taita Hills constitute a distinct biogeographical unit (Stuart *et al.* 1993, Brooks *et al.* 1998, Cordeiro 1998); they are not considered further in this paper.

The mountains are fault blocks of crystalline rock, shaped through tens of millions of years with a final uplift 7 million years ago (Griffiths 1993). The direct climatic influence of the Indian Ocean, which continually sends warm humid air currents over the escarpments, characterises the Eastern Arc ecosystems. This predictability has allowed persistence of the unique forests covering the mountains (Lovett 1993). The mountain peaks reach 2200–2600 m in elevation, and were originally completely forest clad. The Eastern Arc forest type is a combination of Afromontane rain forest and Zanzibar-Inhambane transitional or lowland forest (Lovett 1990). Altitudinal change in forest composition is very gradual and boundaries between montane, submontane and lowland zones are mainly applied by convention (Lovett 1993, 1996).

Four different mountain ranges were visited in 1995–96 and 1996–97 at the end of the dry season (around November–December). This corresponds to the beginning of the breeding period (Moyer 1993), and thus most species are expected to be in their breeding habitat. The areas visited were all on east-facing escarpments. The habitat information below was taken from Collar & Stuart (1988), Jensen & Brøgger-Jensen (1992), Lovett & Pócs (1993), Fjeldså & Rabøl (1995), Svendsen & Hansen (1995), Lovett (1996) and Fjeldså (1999) as well as my own observations. The study areas were:

- 1 Udzungwa Scarp Catchment Forest Reserve in the Udzungwa Mountains. With around 500 km² of forest the Udzungwas have by far the largest forested area in the Eastern Arc and, together with the Usambaras, are the range richest in species. Udzungwa Scarp is the south-eastern part of the range and at 230 km² it is the largest single forest block in the Eastern Arc. The unbroken forest gradient extends from 300 m to around 2100 m, but the lowest elevations are degraded. Annual rainfall is around 2500 mm. Data were collected in December 1995 and January 1996, from seven sites between Chita, on the edge of the Kibashira swamps, and the villages of Uhafiwa and Masisiwe in the highlands. The highest site (2030 m) was in a bamboo zone with remnants of montane forest interspersed.
- 2 Nguru South Forest Reserve. This reserve holds 120 km² of forest from 500 m to 2400 m, of which the lowest forest is degraded and somewhat fragmented. Annual rainfall varies from 1200 mm to 4000 mm at the highest altitudes (Lovett & Pócs 1993). The study area was in the northern part of the reserve, north of Mhonda Mission. Six sites were

visited along an altitudinal gradient from 860 m to 1950 m in December 1996.

- 3 Uluguru North Forest Reserve, which comprises 84 km² of primary forest from around 1100 m to at least 2200 m. Annual rainfall on the eastern slopes ranges from 2900–4000 mm, and no months receive less than 100 mm. This makes it the most perhumid forest in the Eastern Arc. Data were collected in November 1996 from four sites on a gradient above the eastern village of Tegetero.
- 4 The South Pare Mountains, of which the central part (centred on Mt Shengena) holds 143 km² of forest, but is heavily disturbed from both the east and the west sides. Forest cover starts around 1400 m, but is mostly fragmented at lowest altitudes. The peak (2465 m) is covered with elfin forest. Annual rainfall is 1500–3000 mm, probably the highest in the Pare chain, which is in the rain shadow of the Usambaras. Data were collected in December 1996 and January 1997 at three sites crossing from Chome in the west to Gonja village in the east.

Methods

Relative abundance data were obtained by random walking on paths and other 'leading lines' where quiet walking is possible. Observations were made in a 1-km² site, as described in Fjeldså (1999). Altitude was measured with Avocet and Eschenbach altimeters. Because of the steep terrain altitude was allowed to deviate by 50 m within the site. An effort was made to cover each part of the observation site equally and at all hours of the day. Each observed (seen or heard) individual bird was recorded, and observations were made throughout the day. This is necessary to observe both dawn-singing skulkers and sun-loving canopy-species like sunbirds or tinkerbirds. Therefore, from the community of resident species owls were the only group not represented. A standard of 500 individual observations was obtained from each site, though only 450 were recorded at 2030 m on the Udzungwa Scarp in a bamboo zone with very few birds.

Density data are from 10-minute counts of all individuals (of all species) in 1-hectare plots in peak activity hours 06:00 to 09:00 and 16:00 to 18:00 (Koen 1988). An effort was made to record all birds present in the plot, thereby providing a measure of density. Twenty-five plots (25 ha) were covered at each site and density estimates extrapolated to number of individuals per km² (100 ha).

Further details on methodology are given in Romdal (1998). Taxonomy and nomenclature generally follows Dowsett & Forbes-Watson (1993), though complemented by Keith *et al.* (1992) and Urban *et al.* (1997) where opinions diverge. Other deviations are recognition of South Pare White-eye *Zosterops winifredae* (as in Collar *et al.* 1994) and Black-fronted Bush-shrike *Malaconotus nigrifrons* (as in Zimmerman *et al.* 1998). The systematic order follows Dowsett & Forbes-Watson (1993).

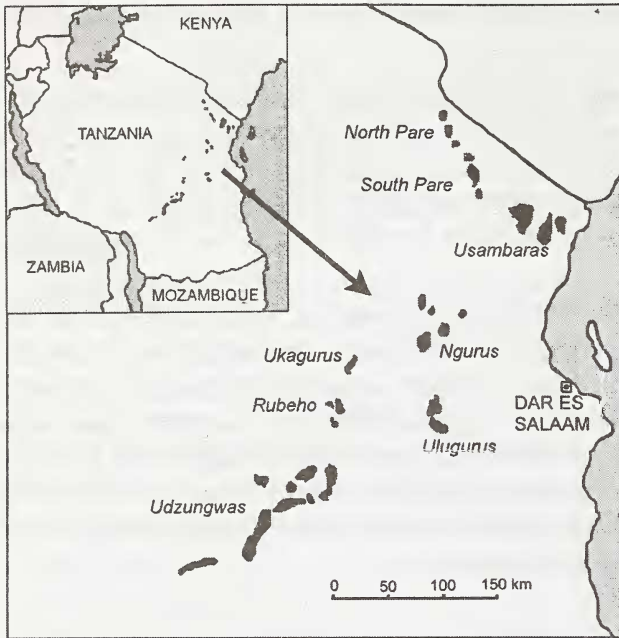


Figure 1. The Eastern Arc Mountain chain of Tanzania. Shaded areas are forested mountain ranges. The four areas visited were Udzungwas, Uluugurus, Ngurus and South Pare Mountains.

Results

Densities

The altitudinal distribution and relative abundance of each species are given in Appendix 1.

The highest overall bird densities were found at mid-altitude, around 1500 m (Table 1). Individual densities (calculated from relative species abundance and overall density, and combined for all four gradients) for the common Eastern Arc species are shown in Figure 2. Typical lowland species such as Red-capped Robin *Cossypha natalensis* and White-throated Nicator *Nicator gularis* are clearly differentiated from montane species such as Eastern Mountain Greenbul *Andropadus nigriceps* and Evergreen Forest Warbler *Bradypterus lopezi*.

Many species showed similar patterns on all the four gradients. An example is White-starred Robin *Pogonocichla stellata* (Figure 3a). The species is montane, but is found below 1500 m in small numbers. In other cases, there were variations that are concealed by the combined curves in Figure 2. The South Pares were particularly distinct in species abundance patterns as well as species composition (see discussion). For example, Bronze-naped Pigeon *Columba delegorguei* (Figure 3b) showed great variation between sites, and occurred at very low densities in the South Pares. (In fact, all three columbid species present in the South Pares were uncommon, perhaps because they depend on intact moist forest while the forest there is relatively degraded.)

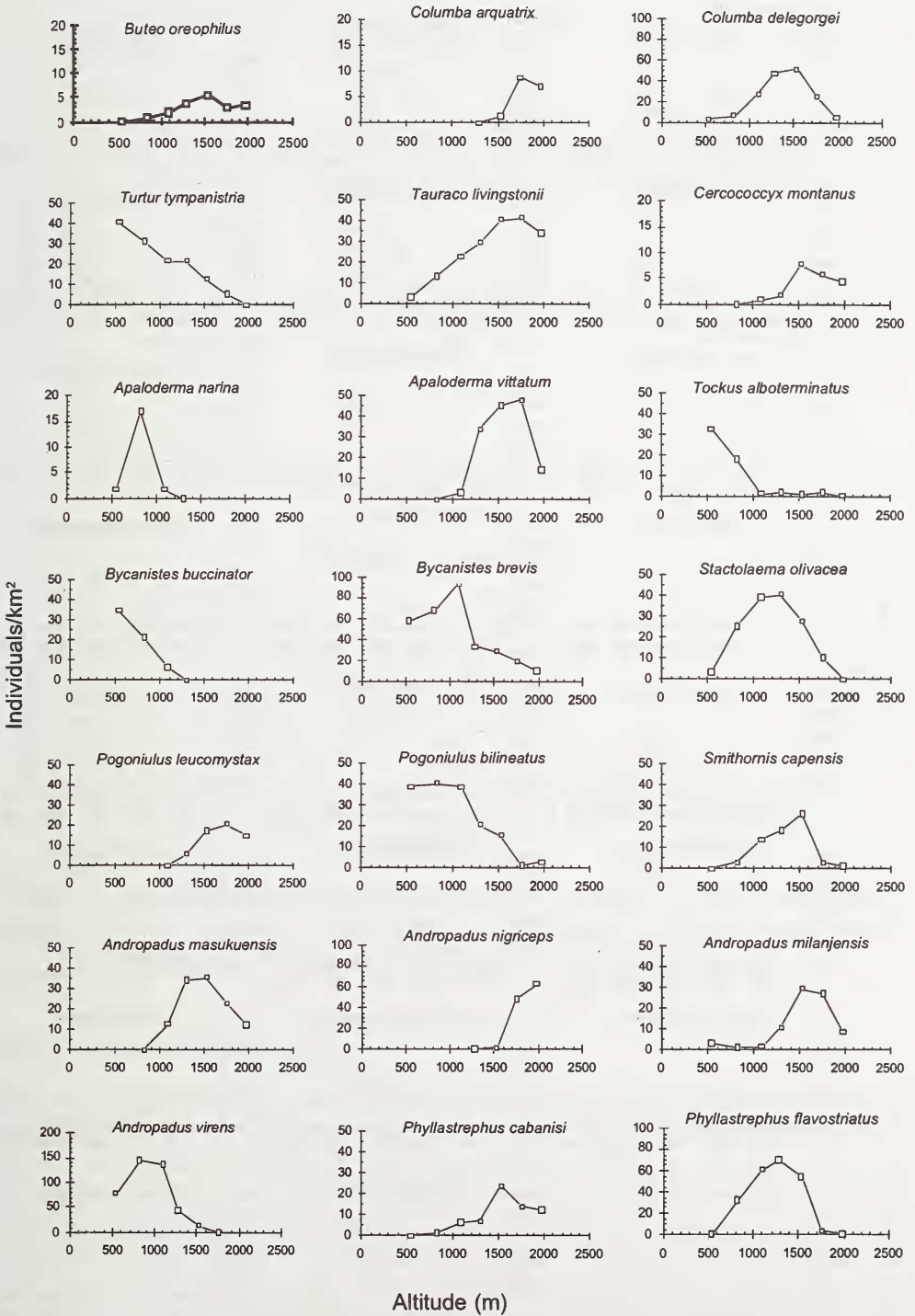


Figure 2. The abundance curves for all common Eastern Arc forest species. The x-axis shows altitude (m) and the y-axis individuals/km². The scale on the y-axis varies. The curves in this figure represent averaged values from all gradients where the species is present.

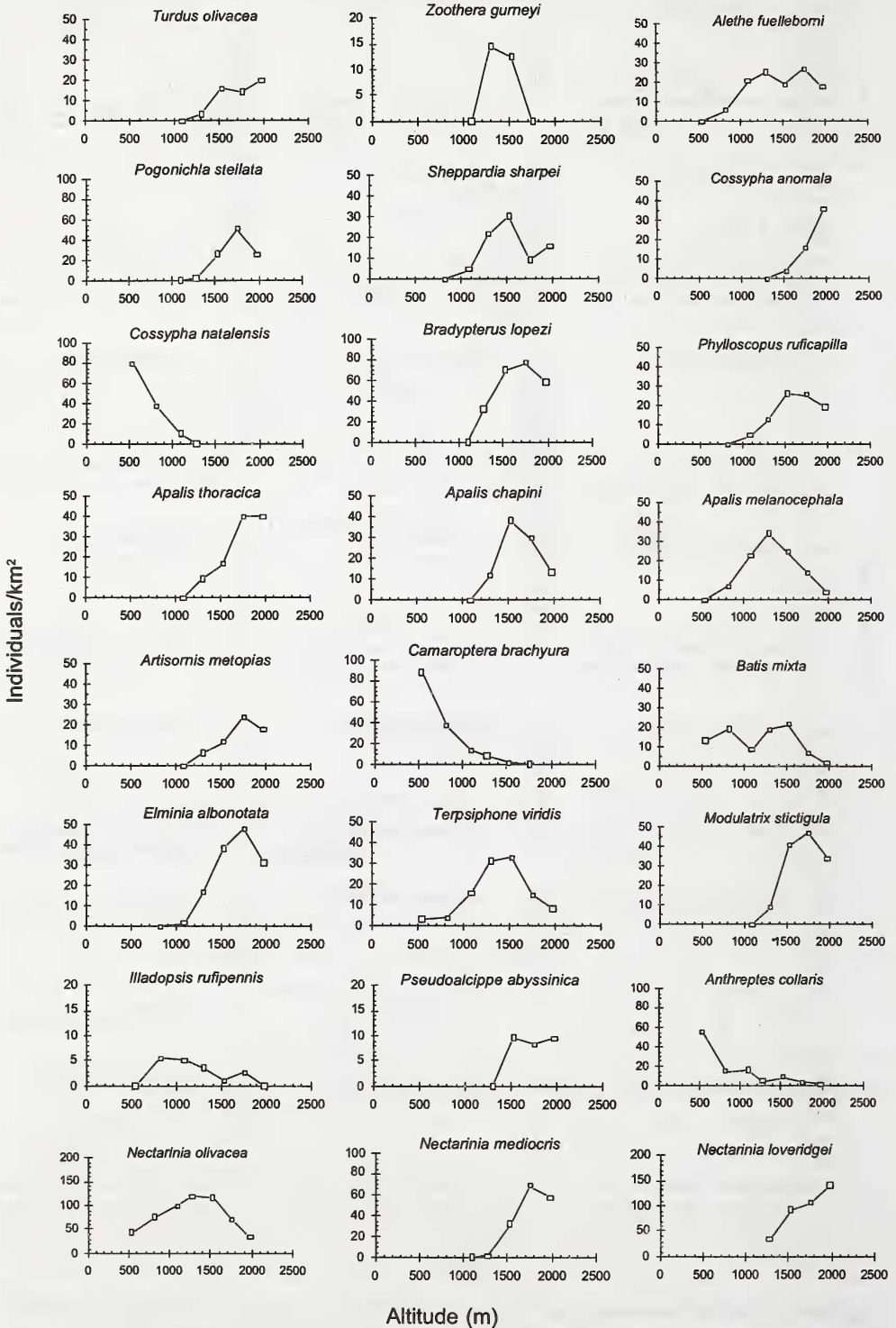


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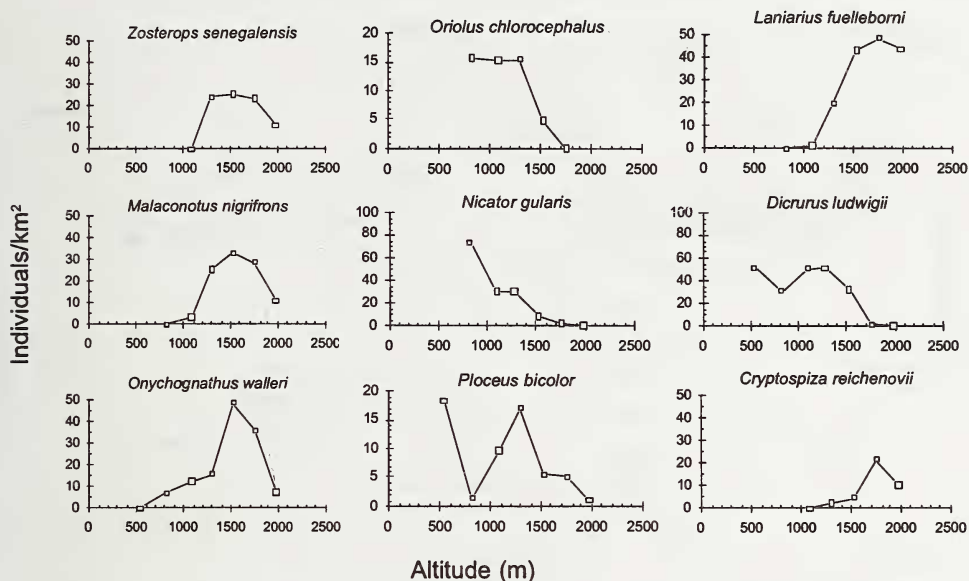


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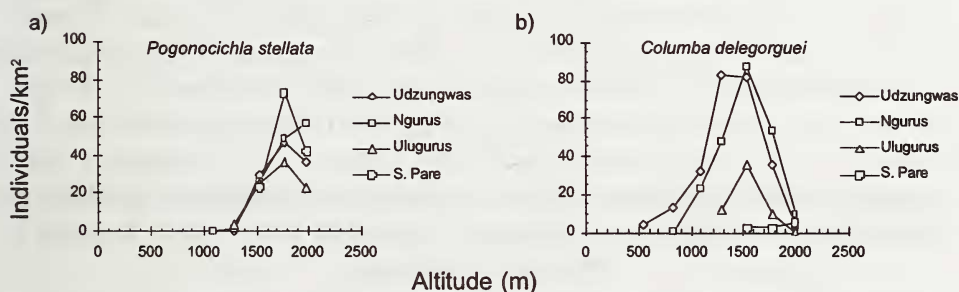


Figure 3. Examples of unmerged abundance curves, showing abundance patterns for each of the four gradients: (a) White-starred Robin *Pogonocichla stellata*; (b) Bronze-naped Pigeon *Columba delegorguei*

Patterns among related species

The patterns of related and possibly competing species are interesting to compare. Hartlaub's Turaco *Tauraco hartlaubi* replaces Livingstone's Turaco *Tauraco livingstonii* in South Pare and other northern ranges, but the abundance patterns of the two species are remarkably similar (Figure 4a). In contrast, while Yellow White-eye *Zosterops senegalensis* is generally a common montane species, South Pare White-eye *Zosterops (poliogaster) winifredae* has succeeded in becoming extremely abundant in the South Pares, its only locality (Figure 4b). Eastern Double-collared Sunbird *Nectarinia mediocris* and Loveridge's Sunbird *Nectarinia loveridgei* are sister species, with *N. loveridgei* endemic to the Ulugurus. The distinctive Moreau's Sunbird *N. (mediocris) moreaui* is probably also a full species (e.g., Collar *et al.* 1994). I found *N. (m.) moreaui* in the Ngurus and South Pares, and nominate *N. mediocris* in the

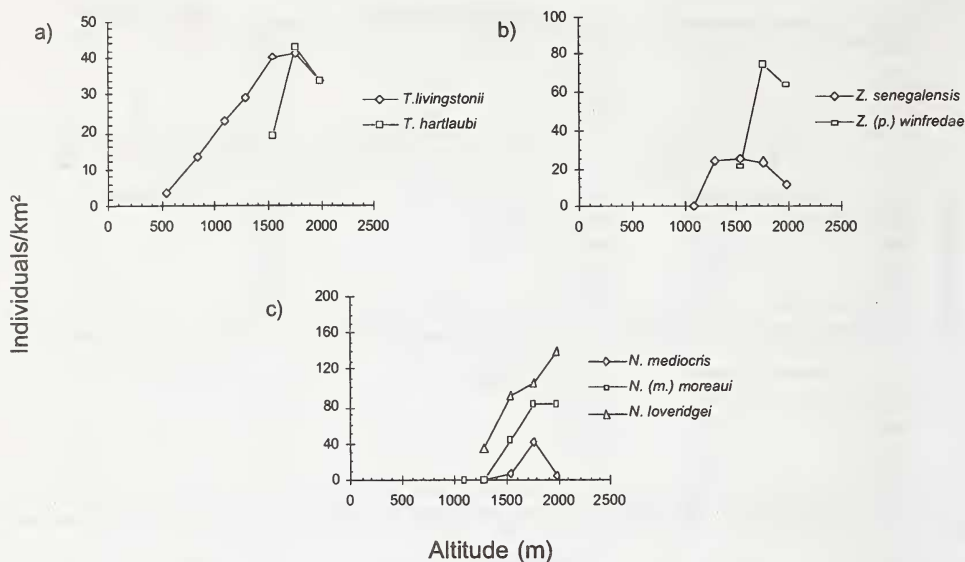


Figure 4. Examples of comparison of abundance patterns of congeneric species in separate mountain ranges: (a) Livingstone's Turaco *Tauraco livingstonii* (data combined from Udzungwas, Ngurus and Ulugurus) and Hartlaub's Turaco *T. hartlaubi* (South Pares only); (b) Yellow White-eye *Zosterops senegalensis* (Udzungwas, Ngurus and Ulugurus) and South Pare White-eye *Z. (poliogastra) winifredae* (South Pares only); (c) Eastern Double-collared Sunbird *Nectarinia mediocris* (Udzungwas), Moreau's Sunbird *N. (mediocris) moreau* (Ngurus and South Pares) and Loveridge's Sunbird *N. loveridgei* (Ulugurus).

Table 1. Overall densities of individual birds at each altitude. In order to present all densities in the same table, nearby altitudes have been lumped. Exact altitudes can be found in Appendix 1

Altitude (m)	Density (birds/km²)			
	Udzungwas	Ngurus	Ulugurus	South Pare
500	916	—	—	—
800	704	776	—	—
1100	896	832	—	—
1300	1252	856	932	—
1500	1244	1224	1168	1052
1700	928	1060	1128	1136
2000	604	800	760	844

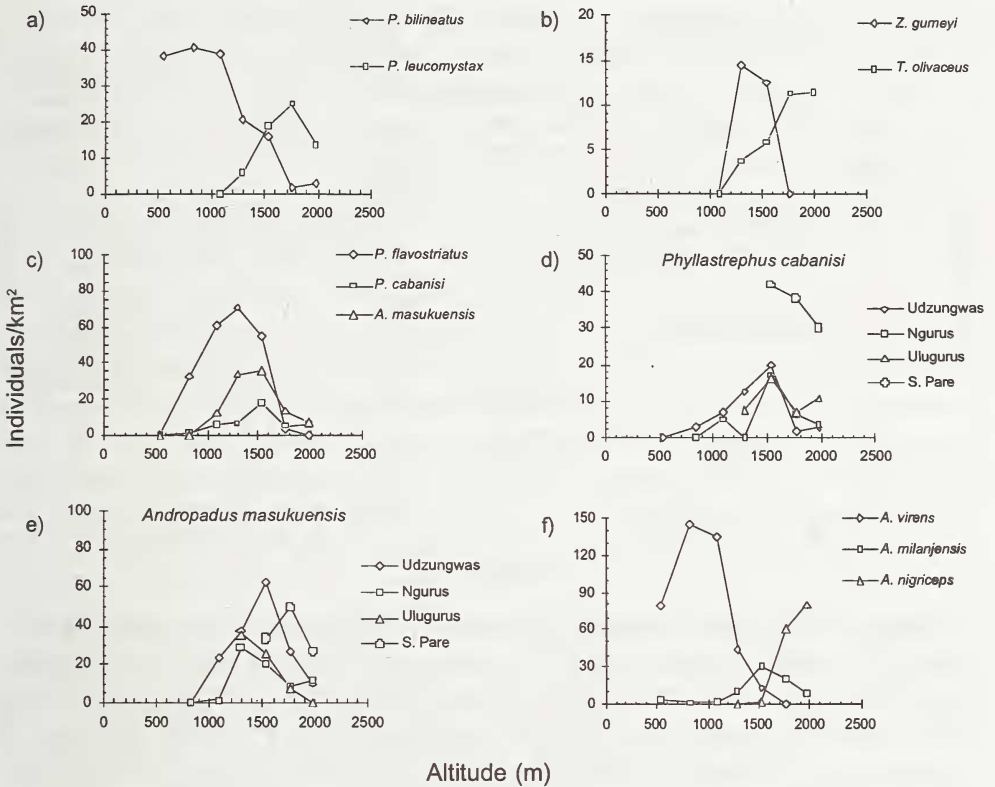


Figure 5. Examples of co-occurrence of closely related species. Data are combined only for the gradients where the species occur together: (a) Yellow-rumped Tinkerbird *Pogoniulus bilineatus* and Moustached Green Tinkerbird *P. leucomystax* (Udzungwas, Ngurus and Ulugurus); (b) Orange Thrush *Zosterops gurneyi* and Olive Thrush *Turdus olivaceus* (Udzungwas and Ulugurus); (c) Yellow-streaked Greenbul *Phyllastrephus flavostriatus*, Cabanis's Greenbul *P. cabanisi* and Shelley's Greenbul *Andropadus masukuensis* (Udzungwas, Ngurus and Ulugurus); (d) *P. cabanisi* on each of the four gradients; (e) *A. masukuensis* on each gradient; (f) Little Greenbul *Andropadus virens*, Stripe-cheeked Greenbul *A. milanjensis* and Eastern Mountain Greenbul *A. nigriceps* (Udzungwas, Ngurus and Ulugurus).

Udzungwas. All three are montane (Figure 4c). The Udzungwa population differs from the others in being uncommon at 2030 m (the census there was centred on bamboo forest, an unfavourable habitat). Apart from that the curves are similar, with the endemic *N. loveridgei* being by far the most common of the three, a parallel to the localised success of *Zosterops winifredae*.

Effects of competition

Competition might limit altitudinal ranges in some cases (Figures 5 and 6). The two tinkerbird species (Figure 5a) are both food generalists, but with a

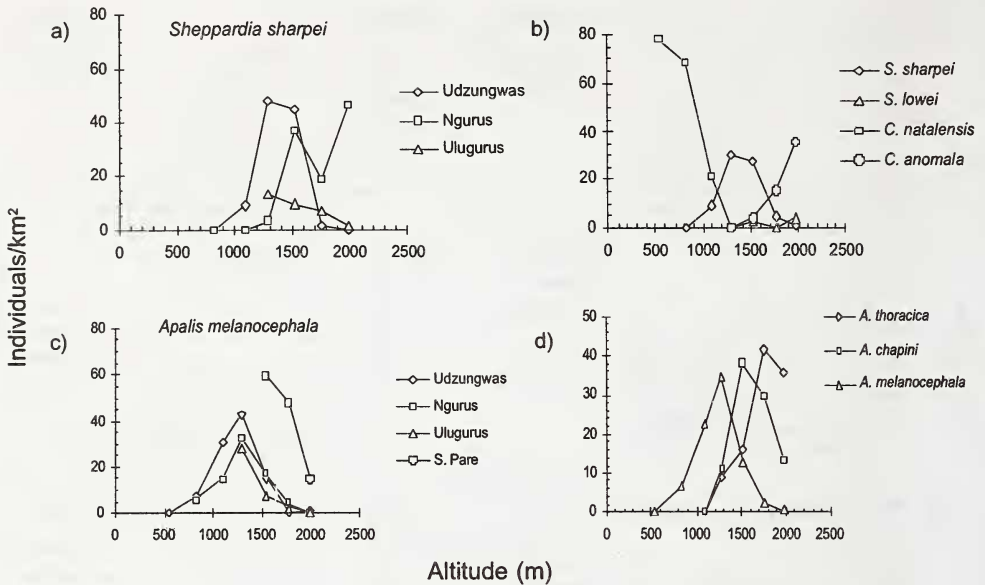


Figure 6. Examples of altitudinal shifts: (a) Sharpe's Akalat *Sheppardia sharpei* (for each gradient where it occurs); (b) *S. sharpei* with Olive-flanked Robin *Cossypha anomala* (combined from Udzungwas and Ulugurus, where they co-occur); Red-capped Robin *C. natalensis* (from Udzungwas, where it co-occurs with the two previous species) and Iringa Akalat *S. lowei* (also from Udzungwas); (c) Black-headed Apalis *Apalis melanocephala*; (d) *A. melanocephala* compared with Bar-throated Apalis *A. thoracica* and Chapin's Apalis *A. chapini* (from Udzungwas, Ngurus and Ulugurus, where the three species co-occur).

Table 2. Extensions to the (approximate) altitudinal ranges found in the literature for East Africa

Species	New records		Range in literature (m)	Comment
	Altitude	Site		
<i>Buteo oreophilus</i>	1100	Udzungwas	1270–3800	Near sea level in Southern Africa
	860	Ngurus		
	1240	Ulugurus		
<i>Andropadus milanjensis</i>	540	Udzungwas	800–2145	Migrant to low altitudes in cold season (Burgess & Mlingwa 2000)
<i>Phyllastrephus debilis</i>	1550	Ngurus	0–1500	
<i>Apalis melanocephala</i>	2030	Udzungwas	0–2000	
<i>Illadopsis rufipennis</i>	1780	Udzungwas	0–1700	
<i>Malaconotus alius</i>	1240	Ulugurus	1300–2100	Very few records
<i>Onychognathus walleri</i>	800	Udzungwas	900–3000	Altitudinal migrant (Burgess & Mlingwa 2000)

preference for mistletoe berries (Jon Fjeldså, pers. comm.). They are typical canopy species and very hard to observe, but both often attend drongo feeding parties. Yellow-rumped Tinkerbird *Pogoniulus bilineatus* is common

at low altitudes, Moustached Green Tinkerbird *P. leucomystax* only at higher altitudes. The two large thrushes, Orange Ground Thrush *Zoothera gurneyi* and Olive Thrush *Turdus olivaceus*, are very similar and are known to compete for food items (Earlé & Oatley 1983). Although they overlap, *Z. gurneyi* is distinctively sub-montane and *T. olivaceus* montane (Figure 5b).

The six common greenbul species have different feeding strategies, with three being mainly or exclusively insect eaters and three having a mixed diet of mainly fruits and berries (described in Dinesen 1997). The two *Phyllastrephus* species are similar and both specialise in searching the vegetation for insects. However, they are segregated mainly by foraging stratum, not altitudinally. Yellow-streaked Greenbul *P. flavostriatus* is found in the canopy, while Cabanis's Greenbul *P. cabanisi* forages on the forest floor and in the understorey. Meanwhile Shelley's Greenbul *Andropadus masukuensis* has specialised in collecting insects from the trunks and branches of trees like a woodpecker, thereby occupying a separate niche. These three species overlap broadly, with *P. flavostriatus* being the most sub-montane (Figure 5c). In the South Pares, where *P. flavostriatus* is absent, *P. cabanisi* and to a lesser extent *A. masukuensis* are particularly common, suggesting some competitive release (Figures 5d and 5e). The three remaining *Andropadus* species have broad diets and are found mainly in the lower strata. They are likely competitors for berries and fruits, and their populations are centred on distinct altitudinal zones (Figure 5f).

Another example of altitudinal exclusion could be Narina Trogon *Apaloderma narina* and Bar-tailed Trogon *A. vittatum* (Figure 2).

Niche shifts

Figure 6 shows two examples where niche shifts through competitive release may have occurred. The averaged data for Sharpe's Akalat *Sheppardia sharpei* suggest it is predominantly sub-montane, peaking around 1500 m. However, when the different populations are viewed together (Figure 6a), it is obvious that the Nguru population is montane (i.e., very common above 1600–1700 m), while Udzungwa and Uluguru populations are more submontane. Figure 6b shows the abundance pattern of *S. sharpei* and of three potential competitors: Iringa Akalat *S. lowei*, Olive-flanked Robin *Cossypha anomala* and Red-capped Robin *C. natalensis*. These are all understorey species and potentially compete for food, especially insects. The two *Cossypha* species are decidedly lowland (*natalensis*) and montane (*anomala*), respectively, and do not overlap. The distribution of *S. sharpei* appears to be intermediate between them. I found very few *S. lowei* in the Udzungwas, which is the only locality for the species in this survey, but it is strictly montane, mainly found at altitudes above *sharpei* (Keith et al. 1992). Evidently the absence of *S. lowei* does not result in *S. sharpei* becoming commoner at high altitudes in the Ulugurus. However, in the Ngurus both *C. anomala* and *S. lowei* are absent, leaving the 'montane small understorey thrush' niche vacant for *S. sharpei* to occupy.

A parallel is seen in the Nguu Mountains, where none of these four thrush species is found. Instead, the coastal lowland species East Coast Akalat *Sheppardia gunningi* is common at all altitudes (Seddon *et al.* 1999). These findings suggest that the *Sheppardia* and *Cossypha* thrushes are in fact competitors.

The South Pare population of Black-headed Apalis *Apalis melanocephala* is strikingly distinct in distribution (Figure 6b), being abundant at montane altitudes. In the other three sites, its pattern of abundance is very similar to those of both its most common congeners, Bar-throated Apalis *A. thoracica* and Chapin's Apalis *A. chapini* (Figure 6c). Of the three, *A. melanocephala* is the least montane, being uncommon above 1500 m. Apalises are quite similar in ecology, but competition should be mainly between *A. melanocephala* and *A. chapini*, as they are both confined to the canopy (see also Urban *et al.* 1997). As *A. chapini* is lacking in the South Pares, that is the probable factor allowing *A. melanocephala* to expand its niche to higher altitudes there.

New altitudinal records

The full altitudinal range of each species is not fully described in a relatively short study like the present one. Some species are recorded to have wider altitudinal ranges in the Eastern Arc forests (Jensen & Brøgger-Jensen 1992, Svendsen & Hansen 1995). Nevertheless, a few records (Table 2) were extensions of known altitudinal range (see Britton 1980, Brown *et al.* 1982, Urban *et al.* 1986, Fry *et al.* 1988, Jensen & Brøgger-Jensen 1992, Keith *et al.* 1992, Svendsen & Hansen 1995, Urban *et al.* 1997).

Distribution patterns among ranges

Appendix 1 shows which species are 'missing' from one particular range while shared among the three others. There are 18 'missing' species in the South Pares, one each in the Ngurus and Ulugurus and none in the Udzungwas. The 'missing' species in the South Pares includes a number of typical Eastern Arc montane species such as *Tauraco livingstonii*, Grey Cuckoo Shrike *Coracina caesia*, *Apalis chapini*, African Tailorbird *Artisornis metopias*, Spot-throat *Modulatrix stictigula*, *Zosterops senegalensis* and Fuelleborn's Black Boubou *Laniarius fuelleborni*. On the other hand, northern species such as *Tauraco hartlaubi* and *Zosterops winifredae* were only found in South Pares.

Discussion

The random-walking method used for this study is a highly rewarding and time-efficient method for obtaining data on species richness, distribution and abundance (Fjeldså 1999). Most sites were surveyed in 3 or 4 days, although more time was required in areas of low bird density. Alternatively one could standardise the effort in terms of data-collecting hours spent walking, but the amount of data will then be very sensitive to weather-induced variations in bird activity.

Actual spot-mapping is the superior method for determining exact densities of individual species, but this will require several weeks spent at each site (Anonymous 1970, Bibby *et al.* 1992). The Udzungwa spot-mapping census of Moyer (1993) suggests that my density measurements in timed counts severely underestimated actual density. My maximum estimate was 626 pairs (1252 individuals) per km², while Moyer (1993) found 1710 pairs per km² at 1450 m in Udzungwa Scarp Forest Reserve. Even though territory mapping can overestimate density when territory holders are assumed to represent a pair or when birds move around, it is the most accurate measure available. The figures presented here should therefore be interpreted as relative, showing the interspecific and altitudinal variation rather than absolute density. Nevertheless, when data on distribution and relative species abundance are needed, a form of random-walking method is recommendable considering the trade-off of data obtained and time spent in the field.

The Eastern Arc spans seven latitudinal degrees and consequently considerable climatic and geographic variations occur. Climatic differences cause variation in the altitudinal span of vegetation belts (Lovett 1993), presumably influencing the ranges of bird species. In this study the South Pares stood out from the other ranges. A number of species had quite different abundance patterns here than in the other sites. In addition, the South Pares lacked many species found in all the other sites. Some of these might have gone locally extinct due to sub-montane habitat loss, but many were true montane forest birds characteristic of the Eastern Arc avifauna. Avifaunally, the South Pares thus seem quite removed from the other sites studied here — as Brooks *et al.* (1998) found for the Taita Hills. A rigorous test of similarities of the complete Eastern Arc avifaunas would be profitable at this time (see also Cordeiro 1998).

The mid-altitude peak of density parallels the peak of species richness on the same gradients (Romdal 1998). This richness pattern is often found on altitudinal gradients, even though traditionally it has been assumed that richness decreases monotonically with altitude (Rahbek 1995). Terborgh (1977) also found mid-altitude peaks for both density and richness in the Andes. One possible explanation is that a zone on the escarpments continuously captures moisture from the humid air meeting the forest, maintaining a high year-round primary productivity that supports many species as well as a high bird density (Jensen & Brøgger-Jensen 1992, Lovett 1993).

Many species' altitudinal ranges extend over most of the gradient, with individual abundance peaks scattered across a range of altitudes. This makes it difficult to delimit communities in intermediate zones: the transition from the lowland to the montane community is gradual. Meanwhile, the graphs suggest some cases of altitudinal replacement of congeners. Historically, these altitudinal segregations could be produced by congeneric competition or by original habitat adaptations of the individual species, or both (Wiens

1989). However, presently competition may control the altitudinal ranges as indicated by the examples of altitudinal shifts.

The primary value of the abundance curves lies in the fact that they clearly show which part of the gradient is most important for each individual species. Many species are known to undertake altitudinal migration in the dry season (Burgess & Mlingwa 2000), but as all my records are from the breeding period the results show the favoured breeding habitat. The range of distributions shows that all parts of the gradient are important for the preservation of forest birds. The considerable variation in abundance demonstrated here possibly reflects 'source' and 'sink' habitat at different altitudes (Pulliam 1988). However, to identify the sources and sinks accurately would require exhaustive data on demography and dispersal (Diffendorfer 1998). The ongoing destruction of forest habitat in the Eastern Arc (through land clearing and timber extraction) is most intense in the lowest parts. This would make species that have their source habitat at lower elevations particularly vulnerable, even when they are also found at higher altitudes. Examples of such species could be *Pogoniulus bilineatus*, Green Barbet *Stactolaema olivacea*, African Broadbill *Smithornis capensis*, Square-tailed Drongo *Dicrurus ludwigii*, *Phyllastrephus flavostriatus*, *Apalis melanocephala* and Dark-backed Weaver *Ploceus bicolor*. Of these, only *Apalis melanocephala* is found in the South Pare Mountains, although suitable habitat is present for all seven. This might be because the lower part of the South Pare gradient is now almost without forest. The recognition of source habitat dependence is obviously crucial for conservation, as preserving sink habitat alone will lead to eventual extinction.

Acknowledgements

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